Effect of titmice (*Parus* spp.) on breeding site preference and breeding success of pied flycatchers (*Ficedula hypoleuca*)

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Forord

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Contents

Abstract

The heterospecific attraction hypothesis suggests that migrants cue on residents with similar ecological needs to find suitable breeding sites, and that they have reproductive fitness benefits from doing so. In northern environments with low resident densities, harsh conditions and unpredictable environments, this has been shown to apply, but further south with more predictable environment and greater resident densities there has been shown both neutral and negative effect of residents on migrants. The aim of this study was to explore if migrant pied flycatchers settled in areas with a higher density of resident titmice than expected by chance, and if the flycatchers that inhabited nest boxes in high-density areas of titmice had higher breeding success than the others. The results suggests a neutral effect of the residents on the migrants; the pied flycatchers apparently settled randomly in relation to titmice, and they did not seem to have higher or lower breeding success in relation to density of neighbouring titmice. The present study area was located at an intermediate latitudinal gradient of other studies suggesting heterospecific attraction and heterospecific competition, and also had an intermediate titmice density between those studies. In the second half of the breeding period, however, the results suggests competition between the pied flycatchers and the titmice, with more pied flycatcher fledglings in low-density areas of titmice. This could be due to the cold and rainy weather in this period, which probably led to less food availability for the coexisting species in the area, which may have turned the neutral interspecific interaction to a negative one. However, there were many confounding variables in this period that may have distorted the results, like the weather, secondary mating status, and breeding phenology of titmice.

Introduction

‘Heterospecific attraction’ was first defined by Mönkkönen et al. (1990) to describe the situation where individuals choose habitat patches by the presence of established individuals of heterospecific species (residents). Heterospecific cues may be profitable if residents reflect the relative quality of patches, if heterospecific aggregations enhance foraging efficiency and reduce predation risk. Choosing habitat based on heterospecific cues may save time and energy compared to sampling actual habitat patches. If time is a limiting factor in reproduction, later-establishing species may gain advantage by using residents as cues (Mönkkönen et al. 1999). This is likely to apply to species breeding in northern environments with harsh, unpredictable conditions, where the densities of residents are below the carrying capacity of the environment (Thomson et al. 2003). Heterospecific attraction require that residents are a reliable sign of patch quality – residents, settling earlier, are probably less time-constrained than colonists and can invest more time in assessing habitat quality; in that case selection would favour individuals using other species as cues, especially among habitat generalists (Mönkkönen et al. 1999). Bertness and Callaway (1994) concluded that positive interactions should be common in communities developing under recurrent physical stress (e. g. in highly variable or seasonal environments) and with high predation pressure, all of which are common factors in northern regions.

Conspecific attraction has been well studied. Doligez et al. (2004) studied conspecific attraction in the collared flycatcher *Ficedula albicollis*, which is both ecologically and taxonomically closely related to the pied flycatcher *F. hypoleuca*. They found that when the collared flycatchers are deciding where to settle in the breeding period, they cue on the conspecifics’ breeding density, which is correlated to patch reproductive success. Individuals may use information by the presence or abundance of conspecifics (Stamps 2001), or by their reproductive performance (Danchin et al. 2001). Stamps (1988) identified four major explanations for conspecific attraction: mating success, predator protection, defence against intruders, and information about the habitat. For heterospecific attraction two of these can also be true: First, aggregated distribution may provide protection against predators by means of cooperative defence or information delivered by neighbours. Slagsvold (1980) showed that presence of the fieldfare *Turdus pilaris* might be favourable for hole-nesting species. The fieldfare evidently served as a strong positive proximate characteristic in the habitat selection and in species like finches *Fringilla* spp., this stimulus may even release a settling reaction outside the normal breeding area. Second, territorial clustering may benefit an individual if settled neighbours reflect the quality of habitat. But it is highly improbable that heterospecific individuals might attract more females or, by means of providing social stimulus, accelerate or improve breeding performance of another species. It is also doubtful that heterospecific individuals would aggregate in order to improve their ability to defend against conspecific intruders or competitors. Some birds benefit by selecting areas containing heterospecifics with whom they can form mixed-species flocks (Mönkkönen et al. 1996). Hino (2000) found that especially subordinate birds benefit from foraging in mixed-species flocks, because the frequency of interference with dominant intraspecifics decreased. Parejo et al. (2005) assumed that migrants are subordinate to residents over nest box acquisition since they arrive later to the breeding area. They studied the heterospecific habitat copying hypothesis, which differs from the heterospecific attraction hypothesis in that it requires environmental predictability (Parejo et al. 2006).

The evidence supporting the heterospecific attraction hypothesis have primary come from Finland; Forsman et al. (2002) found that pied flycatchers breeding in close association with titmice *Parus* spp. initiated breeding earlier, had larger broods and heavier young than solitarily breeding flycatchers, and that the flycatchers preferred to settle close to titmice nests when presented with a choice. Seppänen et al. (2005) showed that brood size declined steeply as a function of hatching date in patches with titmice removed experimentally. In contrast, no decline was observed in the patches with titmice present, suggesting a positive effect from neighbouring titmice. These studies were conducted in a northern area with relative low titmice densities.

By contrast, Gustafsson (1987) found that collared flycatchers had lower fitness when living in close relationship with great tits *Parus major* and blue tits *Parus caeruleus*. Sasvári et al. (1987) also found that a high density of great tits and blue tits had a negative effect on the hatching success and number of fledglings of the collared flycatcher. These two studies were conducted further south with a much higher density of residents than the studies supporting the heterospecific attraction hypothesis. Slagsvold (1975; 1978) documented competition between pied flycatchers and great tits where pied flycatchers made the titmice desert their nest boxes, and where titmice occasionally killed pied flycatchers inside nest boxes. Pied flycatchers and titmice have similar ecological needs, though slightly differing foraging techniques (Lack 1966). Mönkkönen et al. (2004) showed that species interactions might vary in relation to the density of potential competitors and switch from positive to negative along environmental gradients.

The focus species in this study was the pied flycatcher, a small migrant passerine that breeds in many forested areas of the Palaearctic region (Lundberg and Alatalo 1992). The pied flycatcher spends its breeding period in northern areas for the spring and summer, spending the rest of the year migrating or in the wintering areas in tropical West Africa. It prefers nest boxes over natural cavities, making it possible to attract almost the whole breeding population within a woodland to nest boxes (Lundberg and Alatalo 1992). Arriving in the north, it is time-constrained, because of the increasing energy constraints throughout the season that makes the breeding success decline (Siikamäki 1998). Seasonal decline in breeding success can be caused by many factors; one of these is the fact that the pied flycatchers are polygynous and try to attract a secondary female after having attracted one female to a territory. In secondary nests some young often die from malnutrition as a result of low male assistance, and secondary females raise significantly fewer offspring than do simultaneously laying primary females (Alatalo et al. 1985; Stenmark et al. 1988; von Haartman 1958). Most of the secondary females are raising the broods later in the season which could lead to seasonal decline in the breeding population. Another factor causing seasonal decline in breeding success declining food supply throughout the season. The pied flycatchers usually breed two or three weeks after the titmice, so they miss the time when caterpillars are most abundant. The earliest broods in the pied flycatchers are more successful if they can lay their eggs at the same time as the tits (Lack 1966).

The aim of this study was to explore the dynamics between pied flycatchers and titmice. The questions asked were whether pied flycatchers settle closer to titmice nests than expected by chance, and whether the breeding success is higher if the distance to the nearest titmouse is short, or if the titmice density is high.

The dorsal plumage colour of pied flycatcher males vary from conspicuously black to more brown and female-like. The browner males may be accepted to settle closer to conspecifics than blacker males (Slagsvold and Lifjeld 1988), probably because they are regarded less as competition for the already settled males. As Sætre et al. (1994) has shown the pied flycatcher females prefer brightly coloured males, as one of many cues when sampling for a mate (Dale and Slagsvold 1996). Because of this male plumage colour was also investigated to see if there was any relation between the males' choice of breeding site and the males' plumage colour, to explore the possibility of the titmice letting flycatcher males with browner plumage colour come closer.

Methods

The study site

The fieldwork was conducted from April to July 2004 at the study site Dæli (59º56'N, 10º33'E), located west of Oslo, Norway. The site consists of about 440 nest boxes spread out over an area of approximately 160 ha. In 2004 there were 76 pied flycatchers breeding in the nest boxes. Other species that use the nest boxes are great tit, blue tit, and a few coal tits (*Parus ater),* and nuthatches (*Sitta europaea).* The nest boxes are attached to tree trunks about 1.5 m above ground, which makes them easy to inspect. The boxes are made of wood and the entrances are 32 mm in diameter. The main nest predators are great spotted woodpecker (*Dendrocopos major*), weasel (*Mustela erminea*), and cat (*Felis catus*), and main predators of juveniles and adults are pygmy owl (*Glaucidium passerinum*) and sparrow hawk (*Accipiter nisus*). The vegetation is rich and dominated by broad-leaved forest that mainly consists of hazel (*Corylus avellana*), birch (*Betula* spp.), maple (*Acer* spp.), ash (*Fraxinus excelsior*), and elm (*Ulmus* spp.), including areas of more coniferous trees, both pine (*Pinus* spp.) and Norway spruce (*Picea abies*).

The observations

Males were identified based on their dorsal coloration and on the size and shape of forehead patch (Lundberg and Alatalo 1992), and dates of male singing were registered to determine male arrival and male settling preference. Female arrival and female settling preference was determined when nest material was observed in the nest box. For each nest box we recorded the onset of nest building and egg laying, clutch size, hatching date, number of young hatched, and number of young surviving until day 13 after hatching. Measurements of body mass (± 0.1 g with Pesola spring balance) of nestlings were taken 13 days after hatching. To estimate hatching date, a linear regression of body mass of hatchlings with known age was used (T. Slagsvold and R. Tusvik, unpublished data).

From a map of the study area the number of successful titmice (i.e. that had at least one fledgling) living within a radius of 100 meters from every pied flycatcher nest was counted. The time interval between each pied flycatcher's onset of egg-laying and its nearest titmouse's onset of egg-laying was measured, and the distance from each box inhabited by a pied flycatcher to the nearest box inhabited by a successful titmouse was measured.

To explore whether the pied flycatchers actively chose nest boxes in proximity of titmice, the distance and density parameters were analysed against a) observations of singing males early in the spring, as indicator of male settling preference and b) onset of nest building, as indicator of female settling preference. Females may use male song cues when deciding where to settle (Lampe and Espmark 2003).

To explore whether the pied flycatchers living close to titmice had higher breeding success than the flycatchers living far from titmice, the breeding success parameters were compared with distance to nearest titmice and with density of titmice within a 100-meter radius. Breeding success was measured by the following parameters:

a) Time from onset of nest building to the first egg was laid.
b) Clutch size (number of eggs laid).
c) Brood size (number of eggs hatched).
d) Hatching success (number of hatchlings divided by number of eggs laid).
e) Number of nestlings surviving to day 13.
f) Average body mass of young day 13.
g) Failure vs. success of the breeding attempt as a binary variable.

In the following the focus will be on density of titmice as most important factor. The results concerning distance to nearest titmouse are presented in Appendix B.

Number of active nests was estimated as the number of nests with eggs. To explore the significance of male plumage colour on nest box choice, Drost's (1936) scale was used. In pied flycatchers the colour varies from black (score = 1) to brown and female-like (score = 7). Temperature and precipitation-statistics was collected from www.met.no, the website of the Norwegian Meteorological Institute.

Statistical analysis

The statistical program StatView 5.0 was used. The variables were not normally distributed. Non-parametric tests were therefore used. Spearman rank correlation was used to find correlation between data. Comparisons within groups were performed with Mann Whitney *U*-test. To explore the effect of the cold and rainy weather that started 8 June, breeding success parameters were also tested before and after 8 June separately (hereafter referred to as Period 1 and Period 2, respectively) against distance to nearest titmouse and density of titmice. Significance level was set to 0.05.

Results

At 8 June there was a drop in the temperature to 11.9°C (figure 1A). The weather had been constant and favourable the period before this day (Period 1). After this day (Period 2) the mean temperature stayed below the average month temperature from 15 June (which is 14°C) and this lasted for about ten days, in addition there was a lot of rain (Figure 1A). The fledging success declined severely in Period 2 for later to rise, and the hatching success also declined slightly in this period (Figure 1B).

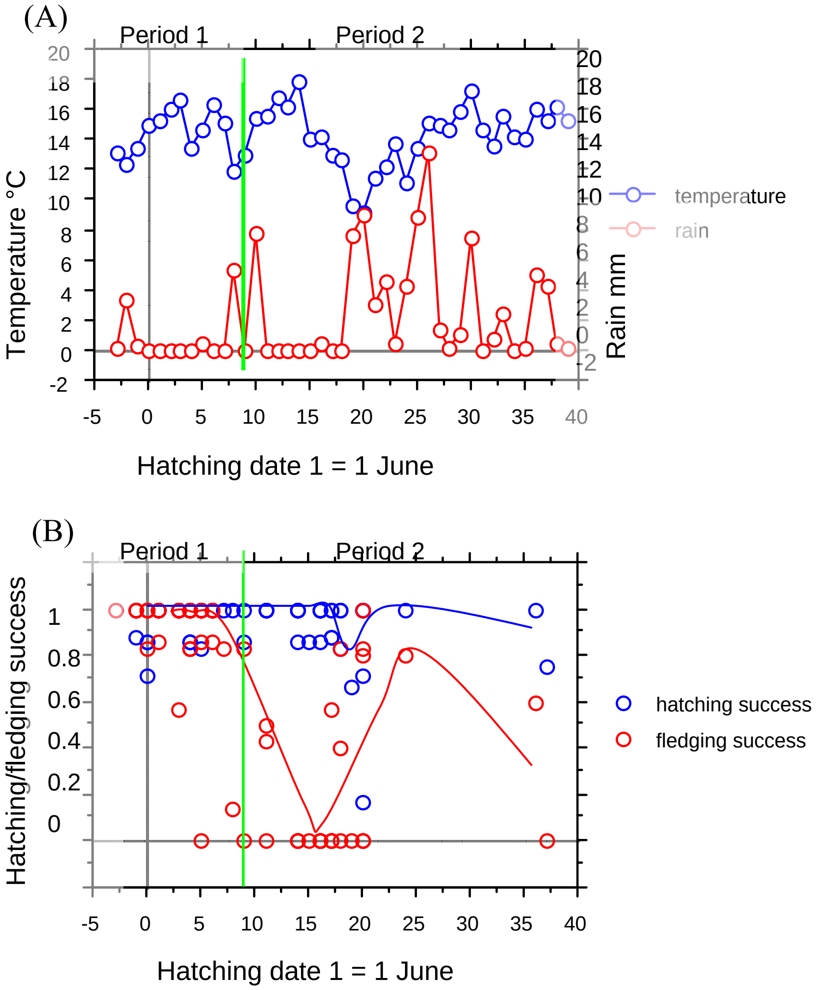

Figure 1. (A): Mean day temperature and mean precipitation in relation to pied flycatcher hatching date. There was a period of cold and rainy weather after 8 June. (B): Hatching and fledging success of pied flycatchers in relation to hatching date. The hatching success declined slightly in Period 2, while the fledging success declined steeply for later to rise. Blue line (hatching success) and red line (fledging success) represent moving average (5 day period). Hatching success = number of hatchlings divided by number of eggs laid. Fledging success = number of fledglings divided by number of hatchlings. Vertical green line in (A) and (B) divides Period 1 (before 8 June) and Period 2 (from 8 June and later).

Of the 180 egg-laying birds other than pied flycatchers, there were 88 blue tits, 83 great tits, 4 coal tits and 4 nuthatches nesting in the nest boxes. All the nuthatches failed breeding. There were 184 nest boxes (42% of all nest boxes) that stayed empty the whole season. The 128 successful titmice (i.e. that had at least one fledgling) laid eggs from 13 April to 1 June (mean: 2 May), and the pied flycatchers laid eggs from 9 May to 20 June (mean: 20 May). The average density of titmice was 1.13 titmice nests ha^{-1} and the average pied flycatcher density was 0.48 flycatcher nests ha^{-1}. The density of titmice within a 100-meter radius from each pied flycatcher nest ranged from 1 to 9 titmouse nests, with a mean value of 3.8 titmice (Appendix A). Density of titmice did not correlate with egg-laying date (Figure 2, Table 1a) or hatching date (Table 1a).

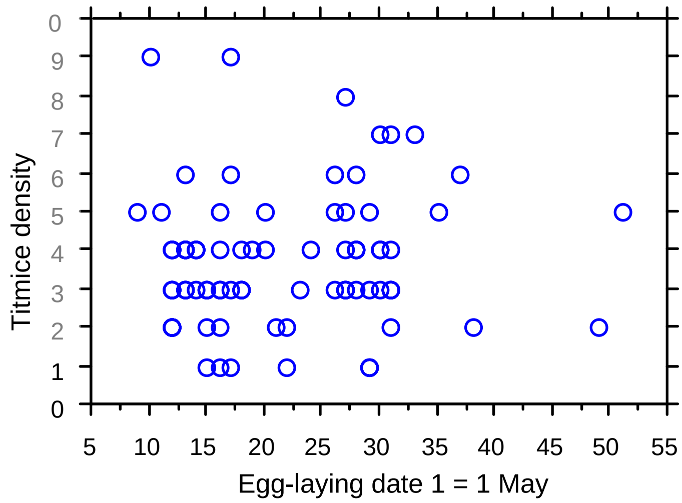

Figure 2. Number of titmice within 100 m radius of each pied flycatcher nest, in relation to egg-laying date of pied flycatcher.

Choice of breeding site

Male choice

Male pied flycatchers' choice of breeding site was investigated by date of male singing near an empty nest box. Singing males were registered near 34 different empty nest boxes. Many of these nest boxes were not later utilized by the pied flycatchers (or any other birds). There was a positive correlation between date of male singing and number of titmice within a 100 m radius (Figure 3, Table 1a); the earliest males sang in areas with fewer titmice.

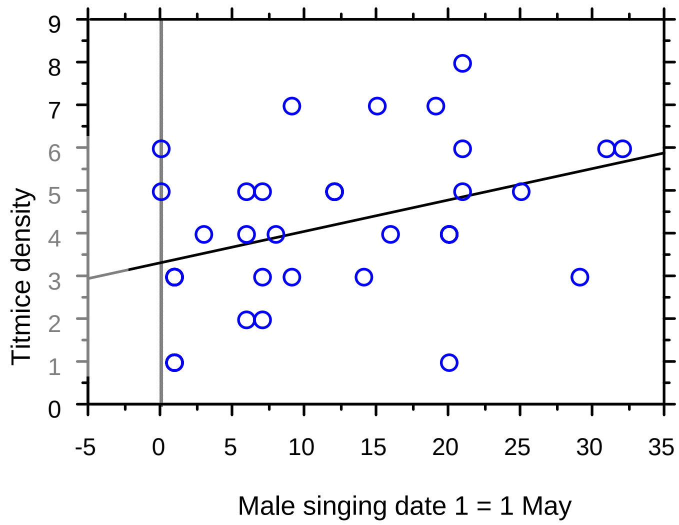

Figure 3. Number of titmice within 100 m radius of each pied flycatcher nest in relation to the date of male singing. Regression line is indicated.

Female choice

Female pied flycatchers' choice of breeding site was investigated by onset of nest building. The onset of nest building was not correlated with density of titmice within a 100 m radius (Table 1a).

Breeding success

Time interval from nest-start date to egg-laying date

The number of days from onset of nest building to the first egg laid by pied flycatchers ranged from 4 to 41 days. The nest-egg interval was not correlated with density of titmice (Table 1b).

Table 1. Results from Spearman rank correlation, comparing flycatcher fitness parameters with dates and time intervals, density of titmice with time, and flycatcher fitness parameters with density of titmice.

		N	r_s	*P*-value ≤
a	Male singing date * density	34	0.39	0.03
	Nest-start date * density	77	0.11	0.32
	Egg-laying date * density	76	0.10	0.40
	Hatching date * density	69	0.04	0.73
b	Nest-egg interval * density	76	–0.21	0.07
c	Clutch size * egg-laying date			
	All	76	–0.50	0.0001
	Period 1	37	–0.34	0.04
	Period 2	39	–0.66	0.0002
	Clutch size * density			
	All	76	–0.11	0.36
	Period 1	37	0.20	0.24
	Period 2	39	–0.21	0.23
d	Brood size * hatching date			
	All	76	–0.39	0.001
	Period 1	37	–0.03	0.88
	Period 2	39	–0.55	0.002
	Brood size * density			
	All	76	–0.02	0.85
	Period 1	37	0.24	0.16
	Period 2	39	–0.08	0.61
e	Hatching success (%) * hatching date			
	All	69	–0.15	0.23
	Period 1	37	0.15	0.36
	Period 2	32	–0.24	0.18
	Hatching success (%) * density			
	All	76	0.01	0.95
	Period 1	37	0.20	0.22
	Period 2	39	–0.11	0.54
f	Nestlings day13 * hatching date			
	All	69	–0.70	0.001
	Period 1	37	–0.12	0.46
	Period 2	32	0.19	0.30
	Nestlings day13 * density			
	All	69	–0.09	0.47
	Period 1	37	0.26	0.12
	Period 2	32	–0.32	0.08
g	Body mass * hatching date			
	All	49	–0.54	0.0002
	Period 1	37	–0.30	0.08
	Period 2	12	0.06	0.83
	Body mass * density			
	All	49	–0.09	0.53
	Period 1	37	–0.20	0.23
	Period 2	12	0.25	0.41

Clutch size

Only one of the 77 nest boxes with nests built by pied flycatchers was deserted before the onset of egg laying. The 76 active nests had minimum 4 and maximum 8 eggs, with a mean value of 6.6 eggs. The clutch size declined significantly throughout the season (Table 1c). Clutch size did not correlate with density of titmice (Figure 4, Table 1c).

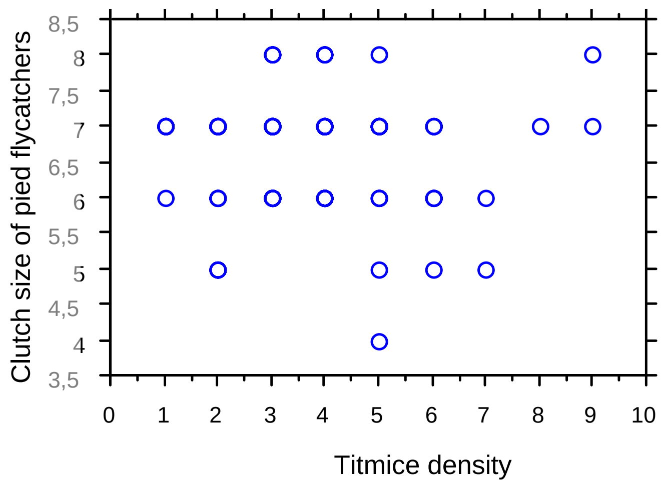

Figure 4. Clutch size of pied flycatchers in relation to density of titmice within 100 m radius of each pied flycatcher.

Hatching success

Of 76 nests with pied flycatchers laying eggs in them, 69 (90.8%) had one or more eggs that hatched. The hatching success (number of hatchlings divided by number of eggs laid) of successful pied flycatchers ranged from 17% to 100%, with a mean value of 94%. Hatching success did not correlate with hatching date or with density of titmice (Table 1e).

Brood size

In Period 1 the brood size ranged from 4 to 8 eggs, and in Period 2 the brood size ranged from 0 to 7 eggs. All nests tested, and tested separately in Period 2, the brood size correlated negatively with hatching date (Table 1d). Brood size did not correlate with density of titmice (Table 1d).

Number of nestlings at day 13

Of the 69 nests with pied flycatcher hatchlings, 49 (71%) had nestlings surviving until day 13. The number of nestlings on day 13 declined in relation to hatching date (Table 1f). Number of nestlings did not correlate with density of titmice (Figure 5, Table 1f), although there was a non-significant tendency for the pied flycatchers living in areas with low titmice density to have more surviving nestlings on day 13 in Period 2 (Table 1f).

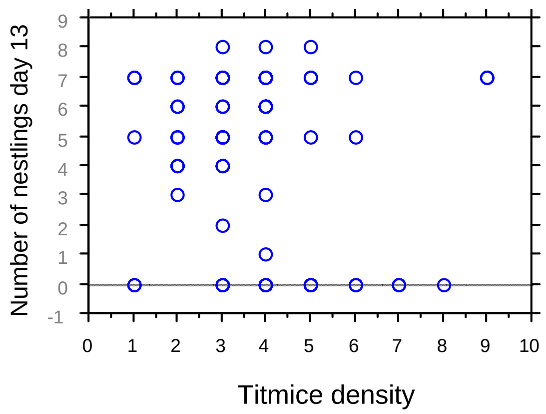

Figure 5. Number of pied flycatcher nestlings at day 13 after hatching in relation to density of titmice within 100 m radius of each pied flycatcher nest.

Body mass

The average body mass per nest of the pied flycatcher nestlings at day 13 ranged from 8.5 g to 15.5 g with a mean body mass of 13.41 g. Nestling body mass strongly declined throughout the breeding season. The body mass did not correlate with density of titmice (Figure 6, Table 1g).

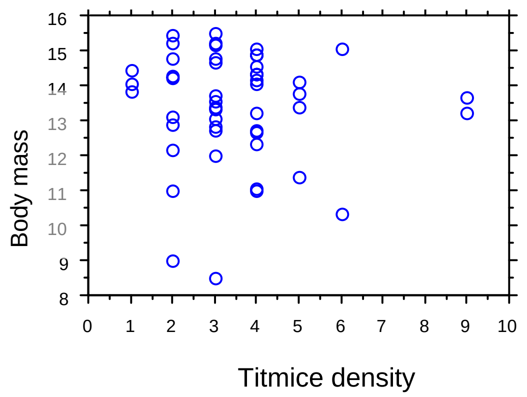

Figure 6. The average body mass per nest of the pied flycatcher nestlings at day 13 after hatching in relation to the density of titmice within 100 m radius of each pied flycatcher.

Fledging success measured as fledged vs. failed

Only the pied flycatchers that had minimum five hatchlings had at least one fledgling. 48 of the 69 nests with hatchlings (69.6%) had one or more fledglings. When comparing the flycatcher nests that had at least one fledgling with the ones with total failure in relation to hatching date, it showed a strong correlation (Table 2); the ones that hatched late had fewer fledglings. In Period 1 only one nest had total fledging failure. 20 nests failed and only 12 nests had one or more fledglings in Period 2, and nests with young fledged were located in areas with a lower density of titmice than nests with total failure in this period (Figure 7, Table 2). All nests tested this was still significant (Table 2).

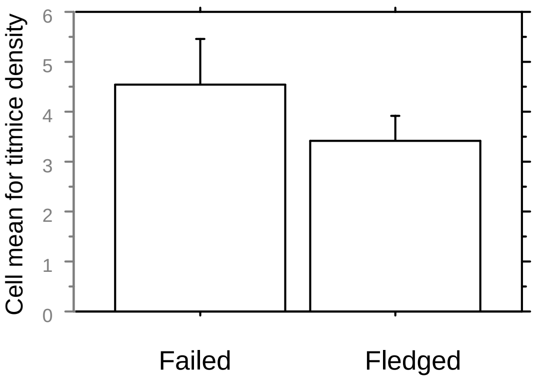

Figure 7. Density of titmice within 100 m radius of each pied flycatcher nest in relation to pied flycatcher nests with total failure ('Failed') and pied flycatcher nests with one or more fledglings ('Fledged') in Period 2. Error bars: 95% Confidence interval.

Table 2. Mann–Whitney *U*-test comparison between pied flycatcher nests that had one or more fledglings ('Fledged') and nests with total failure ('Failed') in relation to density of titmice within 100 m radius from each pied flycatcher.

Variable	Fledged vs. failed	*N*	*Z*	*P*-value ≤
Hatching date				
All		69	–4.5	0.0001
Period 1		37	–0.993	0.32
Period 2		32	–0.78	0.43
Density				
All		69	–2.51	0.01
Period 1		37	–1.49	0.14
Period 2		32	–1.995	0.05

Male plumage colour

The dorsal plumage colour of 50 pied flycatcher males was mapped, 31 in Period 1 and 19 in Period 2. The colour of the males ranged from 1.5 (blackest) to 7 (brown and female-like), with a mean of 3.3. Male plumage colour did not correlate with density of titmice (Figure 8, Table 3), but correlated negatively with number of nestlings on day 13 (Table 3); the darker males had more nestlings than the browner ones. The male plumage colour correlated positively with time from the nearest tit's first egg to each pied flycatcher's first egg; in the nests where the males were darker the onset of egg laying was sooner after the titmice than the nests with browner males (Table 3). In Period 1 male plumage colour correlated negatively with clutch size (r_s = –0.44, N = 31, P = 0.02), brood size (r_s = –0.37, N = 31, P = 0.05) and number of nestlings day 13 (r_s = –0.36, N = 31, P = 0.05); the nests with blacker males had more eggs, more hatchlings and more fledglings in this period. In Period 2 the male plumage colour was not correlated with any variable.

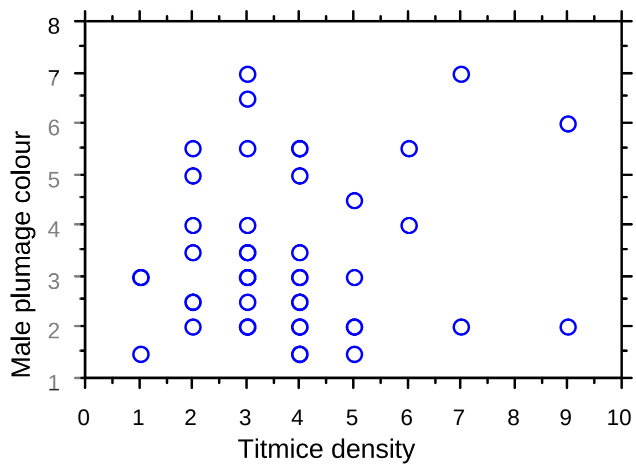

Figure 8. Male plumage colour in relation to density of titmice within 100 m radius from each pied flycatcher nest.

Table 3. Male plumage colour tested with Spearman rank correlation against breeding success parameters, dates and density of titmice within 100 m radius of each pied flycatcher.

Male plumage colour vs.	N	r_s	P-value ≤
Nest-start date	50	0.19	0.19
Nest-egg interval	50	–0.01	0.97
Egg-laying date	50	0.20	0.17
Egg-laying interval	50	0.32	0.03
Hatching date	50	0.22	0.14
Clutch size	50	–0.25	0.08
Brood size	50	–0.23	0.10
Nestlings day 13	50	–0.35	0.02
Body mass	50	–0.12	0.44
Density	50	0.02	0.89

Time interval between each pied flycatcher's first egg and the nearest tit's first egg

In Period 1 there was no correlation between hatching date and egg-laying interval, but in Period 2 the number of days between the nearest titmouse's first egg and each pied flycatchers' first egg augmented significantly with time (Figure 9, Table 4). Consequently most of the titmice had fledged when the pied flycatchers in Period 2 hatched. There was no correlation between egg-laying interval and density of titmice in Period 1 (Table 4).

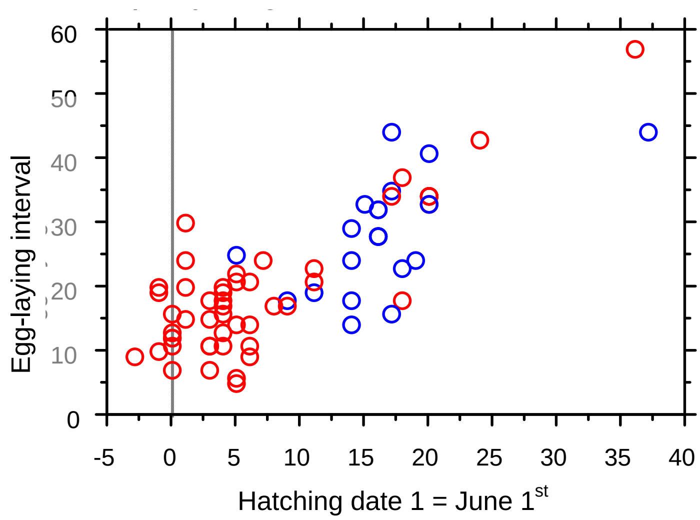

Figure 9. Egg-laying interval in relation to hatching date of pied flycatchers. Egg-laying interval = number of days between each flycatcher's first egg and its nearest titmouse's first egg. Red dots: One or more flycatcher fledgling. Blue dots: Total fledging failure.

Table 4. Spearman rank correlation comparing egg-laying interval with hatching date of pied flycatchers and density of titmice within 100 m radius from each pied flycatcher nest. Egg-laying interval = number of days between each flycatcher's first egg and its nearest titmouse's first egg.

Egg-laying interval vs.	*N*	r_s	*P*-value ≤
Hatching date			
All	69	0.71	0.0001
Period 1	37	0.14	0.40
Period 2	32	0.72	0.0001
Density			
All	76	–0.04	0.75
Period 1	37	–0.25	0.13
Period 2	39	–0.13	0.42

Discussion

The heterospecific attraction hypothesis suggests that migrants cue on residents to find a suitable breeding site, and that they have reproductive benefits from aggregating with heterospecifics. This has been shown for migrant pied flycatchers at 64°50'N, 24º30'E with an average resident titmice density of 0.49 pairs ha^{-1} (Forsman et al. 2002; Seppänen et al. 2005). Forsman et al. (2002) also showed an active settling preference by flycatchers for nest boxes located close to a titmouse nest. However, aggregating with heterospecifics can reduce the migrants' fitness if the density is high, as shown by Gustafsson (1987) on migrant collared flycatchers. His study was conducted at 57º10' N, 18º20' E with a high density of resident titmice, up to an average density of 2.71 titmice pairs ha^{-1}. Sasvári et al. (1987) also documented poorer breeding success of migrant collared flycatchers when the resident tit density was high, up to 2.3 titmice pairs ha^{-1} at 47º32'N, 18º55'E. Mönkkönen et al. (2004) showed that species interactions might vary in relation to the density of potential competitors and switch from positive to negative along environmental gradients. They defined Northern Europe to be north of 60°N, representing the boreal biome with harsh winters and low titmice densities (0.2 pairs ha^{-1} in average) with positive interspecific interaction, and Central Europe to be south of 60°N with intermediate titmice densities of 1.2 pairs ha^{-1} in average where the interspecific interaction can switch from positive or neutral to negative, promoting interspecific competition (Mönkkönen et al. 2004).

The study area at Dæli in the present study is located at 59º56'N, 10º33'E with an average titmice density of 1.13 titmice nests ha^{-1} in 2004. The latitudinal location and the density of titmice in my area lie in between of the studies mentioned above showing heterospecific attraction and competition. The results of the present study suggested that there was a neutral relationship between the migrants and the residents. Apparently the pied flycatchers randomly chose nest boxes independent of the density of the neighbouring titmice. The breeding success of the pied flycatchers did not decline or increase by living in an area with many titmice around. The same applied when testing against the distance to nearest titmouse nest (Appendix B). There was no sign of preference for areas with many empty nest boxes either, or areas with more of one tit species than another (R. Tusvik, unpublished results). In a 100-meter radius from each pied flycatcher nest, the number of empty nest boxes ranged from 1 to 11, with a mean value of 4.7 empty nest boxes. Thus, the pied flycatchers had a great variety of settling choices when it comes to density preferences.

The pied flycatcher males showed a significant tendency to sing in areas early in the season. There was no correlation between other settling dates and density of titmice, suggesting that the earliest arriving males possibly preferred areas with fewer titmice.

Exploring the relevance of male plumage colour on proximity to titmice, the results implied neither attraction nor repulsion of pied flycatchers on titmice. Forsman et al. (2002) presumed that pied flycatcher females choose males on the basis of site characteristics rather than male characteristics (Alatalo et al. 1985). But pied flycatcher females actually seem to prefer brightly coloured males (with blacker plumage) (Sætre et al. 1994), although this is only one of many cues when searching for a male (Dale and Slagsvold 1996; Lampe and Espmark 2003). The darker males are usually older and arrive earlier at the breeding site, and the females may sample a few males and their nest site before they settle (Dale and Slagsvold 1996). The nests with the blacker males had more nestlings surviving to day 13, and a strong tendency to have a higher fledging success. In the first period the nests with the blacker males also had larger clutch and brood sizes.

However, this potential neutral effect of residents on migrants only applied in the first half of the season, when the weather was somewhat constant and favourable, and most of the active nests probably had two parents taking care of nestlings. As Alatalo and Lundberg (1984) and Gustafsson (1987) described, cold and rainy weather can lead to limited food availability and turn the interspecific interaction in a negative direction, as my results actually showed; pied flycatchers in close proximity of titmice laid fewer eggs and had consequently fewer hatchlings, and pied flycatchers in high-density areas of titmice had fewer fledglings in this period. This could suggest that the two species normally coexisting peacefully could experience a shortage in food availability and start competing over it. Slagsvold (1975; 1978) reported repeatedly competition between pied flycatchers and great tits. In accordance with this, I did also observe fighting between a male pied flycatcher and a male blue tit outside a nest box, and twice I found dead male flycatchers inside empty nest boxes with no apparent injuries, possibly killed by a titmouse. This was in the early settling period, however, suggesting some competition also in this period, perhaps if nest boxes are of high quality. Female pied flycatchers prefer males that defend a territory of high quality (Dale and Slagsvold 1996).

Another study supporting the suggestion of the weather influence, is the one of Eeva et al. (2002) who compared one pied flycatcher population at 61ºN with one at 69ºN, and found that the southern population was much more sensitive to a drop in temperature than the northern one. The northern population was better prepared for cold weather, the females had gained more weight than the females in the southern population and the northern females laid fewer eggs, probably due to an adaptation to the harsh climate on this latitude. The area in the present study lies closer to the southern area described by Eeva et al. (2002), suggesting that females pied flycatchers at this latitude lay more eggs and use less energy on gathering food reserves because the weather is less unpredictable than further north, and the flycatchers may be adapted to maximize their brood sizes in relation to the expected climate (Eeva et al. 2002).

The sudden rainfall and drop in temperature and the fact that more broods probably were raised by only one single parent in the present study, probably led to malnutrition of the nestlings and low survival. As mentioned in the introduction, secondary females may experience lower breeding success than primary females (Alatalo et al. 1985; Stenmark et al. 1988; von Haartman 1958). The mentioned confounding abiotic factors (weather, secondary females) could distort the results after 8 June.

Another confounding issue is the fact that the latest successful titmouse (i.e. that had at least one fledgling) laid eggs 1 June while the pied flycatchers laid eggs until July. Even though Goodbody (1952) documented that titmice fledglings usually stay close to their nests for one month after fledging, there could still have been fewer titmice around, which makes it less valuable to test fitness parameters against proximity to titmice. The flycatchers might still have used information from the success of neighbouring titmice to decide whether to come back to the same habitat next year (Parejo et al. 2006).

This was an observational study and did not compare the results with an area without titmice. It could therefore be possible that the pied flycatchers preferred to breed in an area with titmice instead of one without, and that they had fitness benefits that did not appear in the results. However, there was a great variation in the present data; within a radius of 100 meters from each flycatcher nest the density of titmice ranged from 1 to 9 titmice and the density of empty nest boxes ranged from 1 to 11, the flycatchers' egg-laying date ranged from 9 May to 20 June and the settling time from 30 April to 2 June. This indicates that there might have been a potential neutral interaction between the pied flycatchers and the titmice in this area, which fits with the suggestion made by Mönkkönen et al. (2004) of species interactions varying qualitatively and switching from positive to negative along environmental gradients. In future studies one could do an experimental study removing titmice from one part of the area and compare the two parts, or compare breeding data from several years with densities.

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Appendix A

Mean and median values, ranges and standard deviations of data collected in the present study. All dates: 1 = 1 May.

	N	Median	Mean	SD	Min	Max
Distance to nearest titmouse						
All	77	37	40	15.75	16	90
Period 1	37	37	42	17.7	21	90
Period 2	40	37	37	13.47	16	85
Density of titmice						
All	77	4	3.8	1.75	1	9
Period 1	37	3	3.6	1.8	1	9
Period 2	40	4	3.9	1.72	1	8
Flycatcher fitness parameters						
Clutch size	76	7	6.6	0.78	4	8
Brood size						
All	76	6	5.72	2.12	0	8
Period 1	37	7	6.65	0.75	5	8
Period 2	39	6	4.85	2.59	0	7
Hatching success	76	1	0.86	0.30	0	1
Nestlings day 13						
All	69	5	4.09	2.94	0	8
Period 1	37	7	6.35	1.01	4	8
Period 2	32	0	1.47	2.14	0	7
Average body mass (g)						
All	49	13.75	13.41	1.6	8.5	15.5
Period 1	37	14.11	13.9	1.13	10.34	15.5
Period 2	12	12.4	11.88	1.89	8.5	15.25
Fledging success	69	0.83	0.61	0.44	0	1
Dates and intervals						
Male singing date	34	10.5	12.53	9.36	0	32
Nest-start date	77	10	13.16	8.35	2	32
Egg-laying date	76	19.5	21.76	8.95	9	51
Hatching date	69	37	40.42	8.58	28	68
Nest-egg interval	76	7	8.81	6.81	4	41
Egg-laying interval						
All	76	20	22.24	11.02	0	57
Period 1	37	15	15.30	5.89	5	30
Period 2	39	29	28.82	10.74	0	57
Male plumage colour						
All	50	3	3.33	1.54	1.5	7
Period 1	31	2.5	3.18	1.57	1.5	7
Period 2	19	3	3.58	1.49	1.5	7

Appendix B

Spearman rank correlation comparing dates, intervals and fitness parameters of the flycatchers with distance from each pied flycatcher to nearest titmouse nest.

Distance vs.	*N*	r_s	*P*-value ≤
Male singing date	34	0.08	0.65
Nest-start date	77	–0.04	0.70
Egg-laying date	76	–0.10	0.36
Hatching date	69	–0.09	0.48
Nest-egg interval	76	–0.01	0.95
Clutch size			
All	76	0.10	0.37
Period 1	37	–0.29	0.08
Period 2	39	0.53	0.003
Brood size			
All	76	0.23	0.04
Period 1	37	–0.04	0.80
Period 2	39	0.32	0.05
Hatching success			
All	76	0.16	0.16
Period 1	37	0.31	0.06
Period 2	39	0.02	0.91
Nestlings day 13			
All	69	0.09	0.45
Period 1	37	0.03	0.88
Period 2	32	–0.03	0.87
Body mass			
All	49	–0.08	0.59
Period 1	37	–0.18	0.29
Period 2	12	–0.16	0.60
Male colour	50	–0.03	0.83
Egg-laying interval			
All	76	0.01	0.92
Period 1	37	0.10	0.56
Period 2	39	0.10	0.53

Mann–Whitney *U*-test comparison between nests that had one or more fledglings (Fledged) and nests with total failure (Failed) of the pied flycatcher in relation to distance from each pied flycatcher nest to its nearest titmouse nest.

Fledged vs. Failed	*N*	*Z*	*P*-value ≤
Distance			
All	69	–0.20	0.84
Period 1	37	–1.33	0.18
Period 2	32	–0.002	0.98